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ECOLOGICAL SEGREGATION AMONG NERITES AT NORTH-WEST CAPE, WESTERN AUSTRALIA

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SUMMARY

The ecological segregation of nerites was examined both horizontally and vertically. Two groups of species were found. *Nerita undata* and *N. chamaeleon* inhabit the rocky shores of the Exmouth Gulf side of North-West Cape where the water has a high silt content. *Nerita plicata* and *N. albicilla* live on the Indian Ocean side of the Cape where water turbidity is low. The temperate species *N. atramentosa* extends as far north as the southern end of North-West Cape, where it occurs sympatrically with *N. plicata* and *N. albicilla*. In each group of species one lives high on the shore (*N. undata* or *N. plicata*) and one is lower (*N. chamaeleon* or *N. albicilla*). Where *N. atramentosa* occurs it occupies an area slightly above *N. albicilla* and below *N. plicata*. These findings are compared with the results of other studies on the patterns of ecological segregation in nerites.

INTRODUCTION

Paine (1962) pointed out that to coexist successfully potential competitors must each utilize one or more aspects of the common environment more effectively than the competing species. If this was not done competitive pressures would lead to the exclusion or modification of the less well adapted species. The mechanisms by which closely related species living sympatrically utilize and partition the available resources have received an increasing amount of attention from marine biologists. Molluscs have been particularly useful in these investigations. The pioneering work of Kohn (1959) on the genus *Conus* on intertidal beachrock platforms in Hawaii is well known. The studies were later extended to other areas of the Indo-Pacific (Kohn, 1966; 1967; 1968). Paine (1962) investigated overlap in the genus *Busycon* in Florida and examined the trophic structure of molluscs in an area of Alligator Harbor, Florida, which had two pairs of congeneric species (Paine, 1963).

In the years since Paine's 1963 paper a number of studies of this type have been conducted on a variety of molluscan groups, including nerites. Nerites are particularly useful for a number of reasons. The family Neritidae has over 200 species worldwide (Russell, 1941). The genus *Nerita* is widely distributed on rocky shores, and there are often several species inhabiting a particular area. The species are moderately large, have high population densities and are well known taxonomically. All are herbivorous; they feed by rasping algae from the rocks on which they live. The ecology and physiological ecology of nerites have been investigated in several areas: the Caribbean Sea (Kolipinski, 1964: Chisslett, 1969; Lewis et. al., 1969; Lewis, 1971), the Red Sea (Safriel, 1969), the Indian Ocean (Hughes, 1971), and Australia (Underwood, 1975; 1976; Coleman, 1976; Wells, 1978).

Shallow-water molluscs exhibit three distributional patterns in Western Australia (Wilson and Gillett, 1971; Wells, 1979). There is a warm temperate fauna on the south coast which extends northwards along the west coast of the state. A tropical fauna on the north coast extends southward along the west coast. The warm temperate and tropical faunas overlap extensively on the west coast. In addition 8 to 9% of the shallow-water molluscs are endemic to Western Australia. Eight species of *Nerita* occur in the state: 7 are tropical, one is temperate, and none is endemic. The area of greatest species overlap of this genus is at North-West Cape, at the extreme northern end of the west coast overlap zone. Five nerites, four tropical and one temperate, are found at North-West Cape (Wells, 1979). It is this area that will be investigated in the present paper.

MATERIALS AND METHODS

Nerites were examined at 10 stations on North-West Cape (Figure 1.) in July and August 1977. Detailed studies were made at Coral Bay (Station 1), Yardie Creek (4), 10 km south of Yardie Creek (3), and Bundegi Reef (8). At each of these stations the intertidal limestone reef had a vertical face which extended from the supratidal area into the lower intertidal region. A gently sloping beachrock platform led from the base of the vertical face into the subtidal zone. Five transects 10 m apart were made at each station. A rope was run from the high tide line down the shore at the bottom of the nerite zone. Beginning at the high tide line a quadrat 3.0 m long and 0.5 m wide was delineated by ropes. All nerites in each quadrat were collected, identified, and measured with calipers. Vertical height on the shore was determined by comparing the level reached at high tide with the tidal prediction for Pt. Murat on the tip of North-West Cape (Australian Hydrographic Service, 1977). The mean difference between successive high and low tides is 1.0 m; the maximum during 1977 was 1.7 m.

Supplementary examinations were made at the six remaining stations (Numbers 2, 5, 6, 7, 9, and 10 on Figure 1). At these stations the beachrock was searched qualitatively to verify the patterns recorded at the four detailed stations. The nerite species present and their positions on the shore were determined.

The overlap of nerite populations on the shore was determined using the index of species overlap developed by Horn (1966). This index is modified from earlier versions proposed by Simpson (1949) and Morisita (1959). The index varies from 1 to 0. A value of 1 signifies complete overlap of populations and 0 indicates complete separation.

RESULTS

Yardie Creek (Station 4)

Three species of nerites, *Nerita undata, N. albicilla,* and *N. plicata* were collected at this station. Both *N. undata* and *N. albicilla* were too rare to be examined quantitatively. *Nerita plicata* was common on the upper shore levels. The mean shell length of this species was 23.7 ± 5.2 mm. Its mean shore height was 2.2 ± 0.4 m. The few *N. albicilla* that were collected averaged 1.8 m on the shoreline, 0.4 m below the average of *N. plicata.*

10 km south of Yardie Creek (Station 3)

Four species were found at this station: *Nerita plicata, N. albicilla, N. atramentosa,* and *N. undata. Nerita atramentosa* and *N. undata* were too rare to be examined quantitatively. The mean shell lengths of the most common species were almost indentical: 20.3 ± 6.5 mm for *N. plicata* and 21.0 ± 2.6 mm for *N. albicilla* (Table 1 and Figure 2). The difference was not statistically

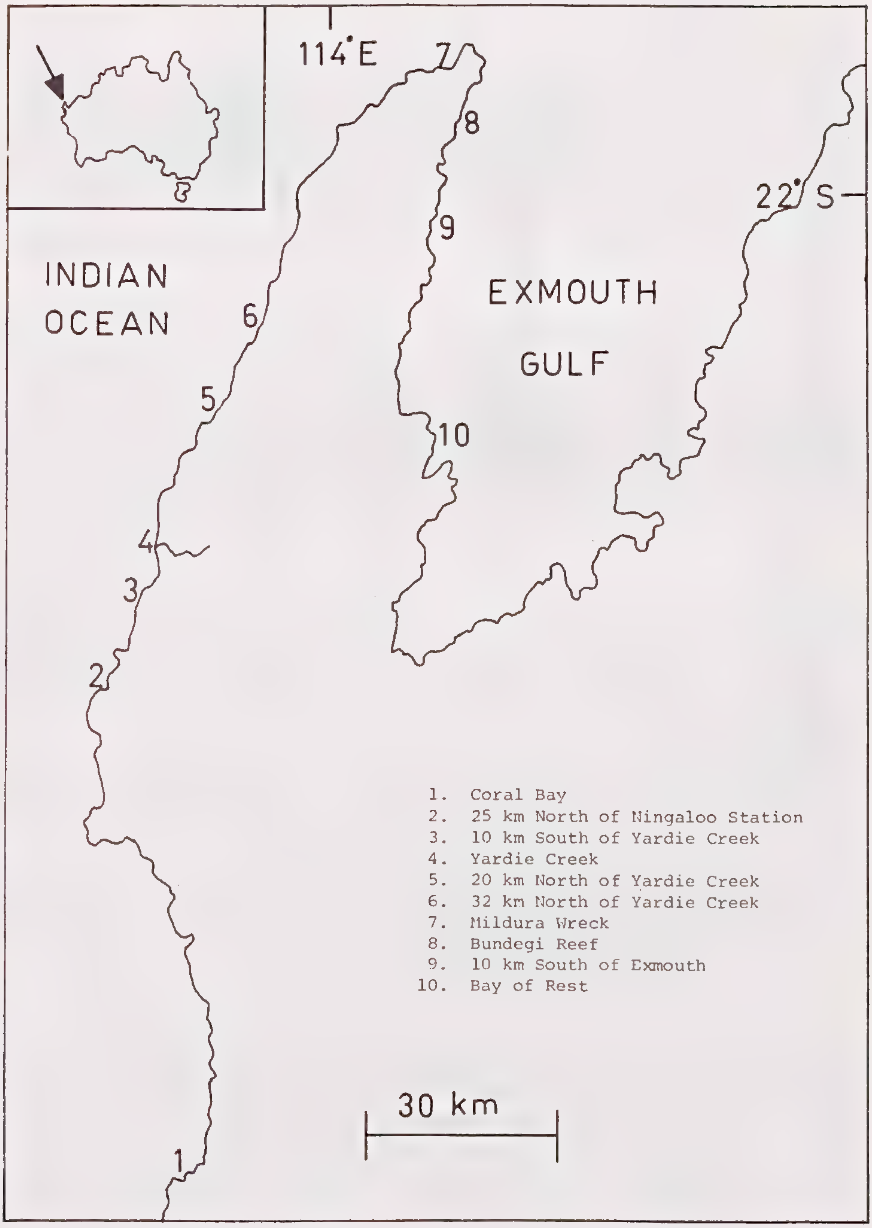

FIGURE 1. Map of North-West Cape, Western Australia, showing the locations of the sample sites.

significant (t-test, 0.05 level). The mean shore heights differed substantially between the two species (Figure 3). *Nerita plicata* averaged 2.6 ± 0.1 m; *N. atramentosa* was 2.0 ± 0.1 m. The vertical overlap on the shore was calculated to be only 0.01.

Coral Bay (Station 1)

Three nerites were found at Coral Bay: *Nerita plicata, N. albicilla* and *N. atramentosa. Nerita plicata* was distributed along the upper intertidal above the level of *N. atramentosa,* but it was rare and did not appear in the quantitative transects. The mean length of *N. albicilla* at Coral Bay was 20.6 ± 1.5 mm. *Nerita atramentosa* averaged 17.9 ± 3.3 mm (Table 1 and Figure 2). The difference was not statistically significant (t-test, 0.05 level). *Nerita albicilla* and *N. atramentosa* occupied overlapping areas on the shoreline (Figure 3). *Nerita atramentosa* was a little higher up, with a mean of 1.9 ± 0.6 m; *N. albicilla* averaged 1.8 ± 0.5 m. The difference on the shore, while consistent, was not statistically significant (t-test, 0.05 level). The index of overlap calculated for the two species was 0.38.

Bundegi Reef (Station 8)

Two species were present at Bundegi Reef: *Nerita undata* and *N. chamaeleon. Nerita undata* averaged 16.5 ± 5.8 mm in shell length and *N. chamaeleon* 13.7 ± 3.9 mm (Figure 4). The difference was not statistically significant (t-test, 0.05 level). *Nerita undata* inhabited the upper intertidal zone and had a mean shore height of 2.1 ± 0.2 m. *Nerita chamaeleon* was lower, with a mean of 1.7 ± 0.4 m (Figure 4). The difference in shore height was statistically significant (t-test, 0.05 level). *Nerita chamaeleon* occupied the lower part of the vertical cliff face, and extended onto the gently sloping beachrock platform below the cliff. The index of overlap between the two species was 0.14

Other stations

The same patterns of nerite distribution were found at the six qualitative stations. At all stations on the west side of North-West Cape (Figure 1, Stations 2, 5 and 6) *Nerita plicata* and *N. albicilla* were the dominant species. *Nerita plicata* always occurred in the upper intertidal zone and *N. albicilla* was below it. Small numbers of *N. atramentosa* were found at Station 2, 25 km north of Ningaloo Station. *Nerita undata* on the upper shore and *N. chamaeleon* on the lower shore were the only two nerites collected at Stations 9 and 10 on the Exmouth Gulf side of North-West Cape.

Thus the stations on the western side of North-West Cape were dominated by *N. plicata* and *N. albicilla;* those on the eastern side were dominated by *N. undata* and *N. chamaeleon.* The key question is whether there is a rapid transition between the two dominant groups at the tip of North-West Cape, or if the transition is gradual. The rocky shore nearest the tip of the Cape was at Station 7, between the northern extremity of North-West Cape and Vlaming Head. Nerites at this station were too scattered to sample quantitatively. A thorough search of the beachrock revealed only *N. plicata* and *N. albicilla.* The nearest rocky shore on the east side of North-West Cape is at Bundegi Reef (Station 8), where *N. undata* and *N. chamaeleon* dominated. Thus the species present on the shoreline switched completely between Stations 7 and 8.

DISCUSSION

The five species of nerites at North-West Cape have been shown to be separable into two groups. The beachrock on the Indian Ocean (west) side of the Cape supports populations of two tropical species: *Nerita plicata* in the upper intertidal and *N. albicilla* lower down. *Nerita atramentosa* occurs at the southern end of North-West Cape where it occupies a shore position intermediate between *N. plicata* and *N. albicilla.* Two other nerites, *N. undata* and *N. chamaeleon,* occur on the Exmouth Gulf (east) side of North-West Cape. *Nerita undata* lives higher on the shore than *N. chamaeleon.* The factors causing the separation of the nerites into distinct groups on the two sides of North-West Cape are unknown, but the situation parallels the distribution of echinoderms in Queensland reported by Endean (1957). The echinoderms were divided into an inshore fauna that lives in areas of high turbidity and low salinity and an offshore group of species that inhabit coral areas of high salinity and low turbidity. Exmouth Gulf has a high turbidity, and much of the shoreline is fringed with mangroves. *Nerita lineata* Gmelin, 1791 is the only nerite occurring in the mangrove

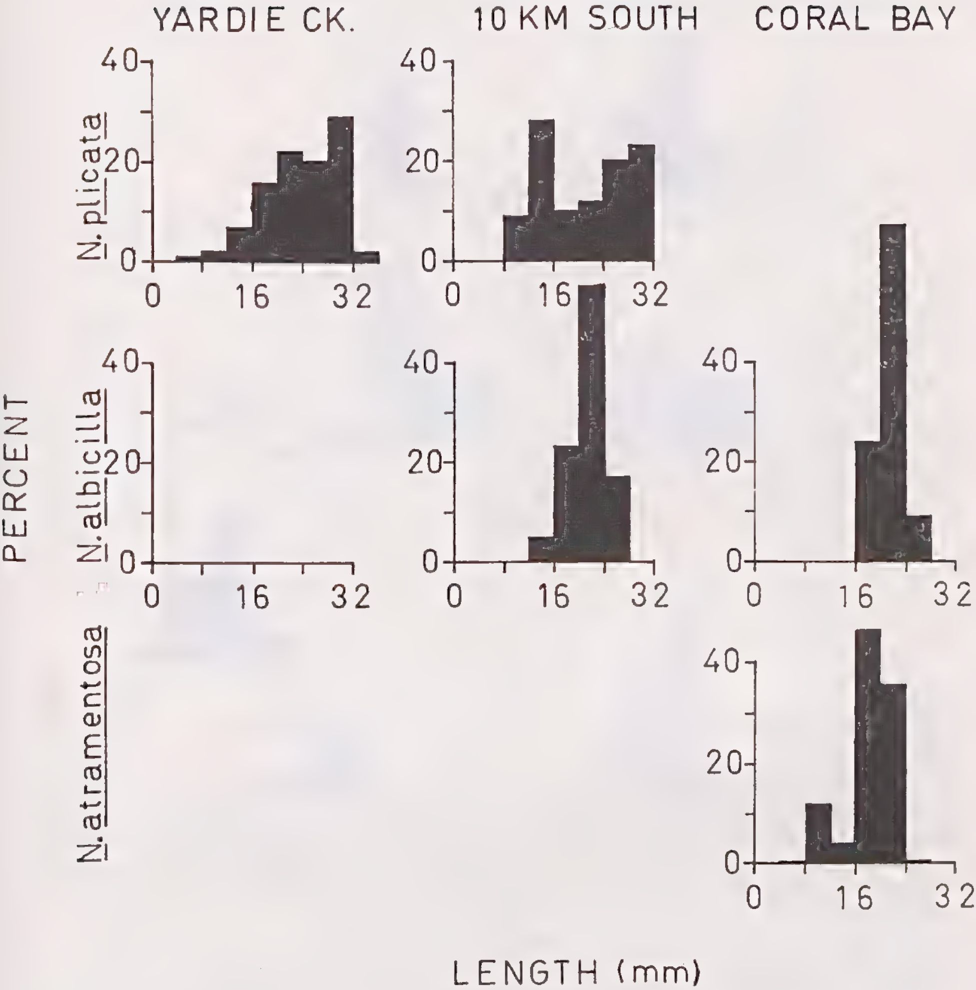

FIGURE 2. Size-frequency graphs of *Nerita* collected at three quantitative stations on the west coast of North-West Cape.

swamps. The waters of the west side of North-West Cape have a low turbidity and the shoreline is fringed with coral reefs.

Differential zonation of nerites on a shoreline is well known (Kolipinski, 1964; Hughes, 1971; Wells, 1978). The study most comparable to the present investigation was conducted in the Admiralty Gulf, Western Australia (Wells, 1978), using the same methods used at North-West Cape. Three nerites were studied on a rocky shore in the Admiralty Gulf. The shore was composed of loose rocks ranging from a few centimeters to 0.3 m in diameter. *Nerita reticulata* Karsten, 1789 had a mean shore height of 3.0 ± 2.5 m; *N. undata* was 3.9 ± 2.6; and *N. polita* Linnaeus, 1758 was 5.2 ± 0.2 m. The index of overlap between adjacent species pairs was 0.29 for *N. undata* - *N. polita* and 0.35 for *N. reticulata* – *N. undata*. Both figures are higher than those of 0.01 recorded 10 km south of Yardie Creek and 0.14 recorded at Bundegi Reef on North-West Cape. The highest overlap found at North-West Cape was for *N. albicilla* – *N. atramentosa*, which had an overlap of 0.38. These species do not occur together over most of their ranges. Thus in both areas of Western Australia that have been studied the nerites show a clear segregation by shore height.

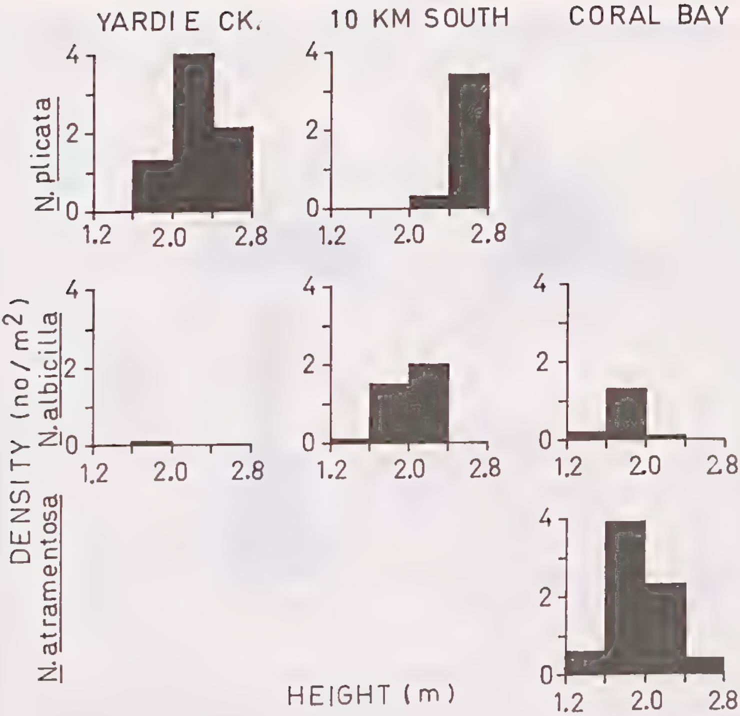

FIGURE 3. Tidal heights of *Nerita* collected at three quantitative stations on the west coast of North-West Cape.

There is some indication that the vertical distribution of *Nerita plicata* on the shore was affected by *N. albicilla*. At Yardie Creek (Station 4), where *N. albicilla* was rare, *N. plicata* was widely distributed between 1.6 and 2.8 m on the shoreline, and had a mean shore height of 2.2 ± 0.4 m. *Nerita albicilla* was common at the station 10 km south of Yardie Creek (Station 3), where it had a mean shore height of 2.0 ± 0.1 m. *Nerita plicata* at this station were higher on the shore than at Yardie Creek. Only a few individuals were found below 2.4 m, and the mean shore height of the species was 2.6 ± 0.1 m, 0.4 m higher than at Yardie Creek.

Congeneric species living at different shore levels where immersion and emersion times are different presumably have different specializations developed to withstand the microenvironments. Little work has been done on this aspect of the biology of nerites. Coleman (1976) investigated the ability of three species (*Nerita albicilla, N. plicata* and *N. polita)* to respire aerially. All three species consumed oxygen at similar rates, indicating that the ability to respire aerially during emersion is not an important factor in determining the vertical distribution of nerite species.

The three species studied in the Admiralty Gulf showed a clear segregation by size: *N. reticulata* averaged 9.4 ± 0.7 mm; *N. undata* 13.0 ± 2.1 mm; and *N. polita* 16.1 ± 1.6 mm (Wells, 1978). The possibility of character displacement similar to that found in mud snails of the genus *Hydrobia* by Fenchel (1975) was suggested. This does not appear to occur at North-West Cape, except possibly at Bundegi Reef, where *N. undata* averaged 16.5 ± 5.8 mm and *N. chamaeleon* were 13.7 ± 3.9 mm.

Densities in the Admiralty Gulf were much higher than at North-West Cape. The maximum density attained by *Nerita undata* at Bundegi Reef was $9.0/m^2$. In the Admiralty Gulf it reached $20.3/m^2$ and *N. reticulata* had a maximum of $35.9/m^2$ (Wells, 1978). The other species at North-West Cape did not have densities greater than $4.0/m^2$. The shorelines of the two areas were different and no doubt affected the *Nerita* populations. The beachrock platforms at North-West Cape are solid cliffs with few nooks and crannies to provide protection for snails. The rocky shore in the Admiralty Gulf had small rocks piled several deep, providing substantial protection. The

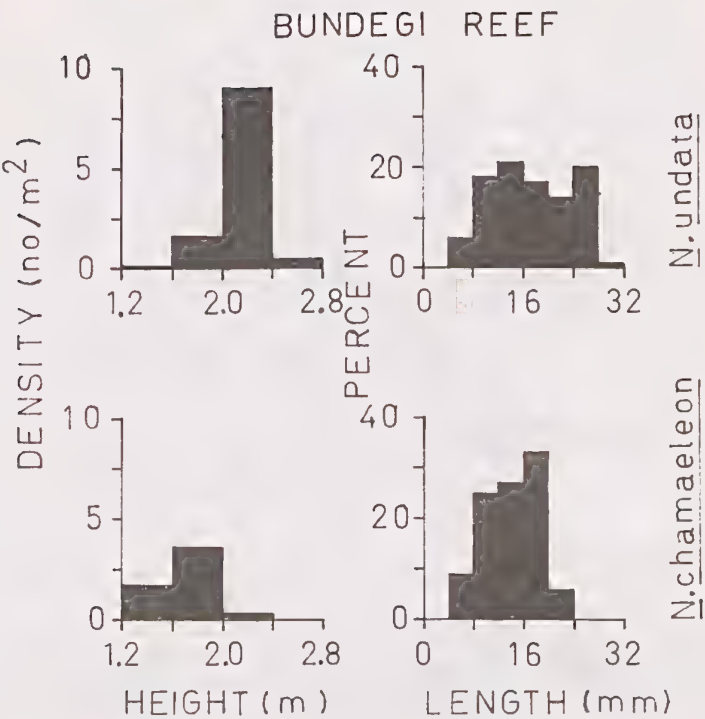

FIGURE 4. Tidal height (left) and size-frequency graphs (right) of *Nerita* collected at Bundegi Reef on the east coast of North-West Cape.

differences in density observed in the two areas could also be a result of differing amounts of food resources along the shorelines. Competition for food amoung congeneric species of carnivorous gastropods is well known (Kohn, 1959; 1966; 1967; 1968; Paine 1962; 1963), but herbivorous species have not been investigated in detail. Underwood (1976) has demonstrated that food competition does occur within populations of *Nerita atramentosa*, and it is quite possible that it also occurs between species.

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Table 1. Population characteristics of nerites collected at North-West Cape.

	Yardie Creek		10 km south		Coral Bay		Bundegi Reef	
	Mean length (mm)	Mean shore height (m)	Mean length (mm)	Mean shore height (m)	Mean length (mm)	Mean shore height (m)	Mean length (mm)	Mean shore height (m)
Nerita plicata Linnaeus, 1758	23.7 ± 5.2	2.2 ± 0.4	20.3 ± 6.5	2.6 ± 0.1	--	--	--	--
Nerita albicilla Linnaeus, 1758	Present	1.8	21.0 ± 2.6	2.0 ± 0.1	20.6 ± 1.5	1.8 ± 1.5	--	--
Nerita atramentosa Reeve, 1855	--	--	Present	Present	17.9 ± 3.3	1.9 ± 0.6	--	--
Nerita undata Linnaeus, 1758	Present	Present	Present	Present	--	--	16.5 ± 5.8	2.1 ± 0.2
Nerita chamaeleon Linnaeus, 1758	--	--	--	--	--	--	13.7 ± 3.9	1.7 ± 0.4

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